

Are There Successional Changes in Arthropod Decomposer Communities?†

M. B. Usher and T. W. Parr

*Department of Biology,
University of York,
York YO1 5DD, U.K.*

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Two kinds of succession could be recognized in the decomposer communities: one is related to habitat change (plant species, micro-environment), and the other to the decomposition stages of the decaying food resource. Both processes are reviewed. Data are given for (a) the decomposition of wood by termites in West Africa, the process being Markovian in character; and (b) the succession of both plants and soil arthropods on the developing chalk soil in Britain, the process largely being studied from measuring changes in the diversity of the communities.

Keywords: ecological succession, Markov processes, transition matrices, diversity, soil arthropods, termites.

1. Introduction

There are potentially two types of succession that could take place in the decomposer communities of an ecosystem. These conceptually different forms of succession are as follows.

(a) The succession imposed on the decomposer community due to the overall change in the habitat, i.e. due to the directionally changing plant structure (old fields → scrub → wood). The imposition of this form of succession is a complex of factors, such as botanical change (affecting the input of the major component of dead material to the decomposer system), micro-environmental changes, and possibly chemical changes.

(b) The succession imposed on the decomposer community by the breakdown of their own resources, i.e. by the loss of structure of a leaf, pine cone, etc.

Whereas the first of these processes has a potential end-point, frequently referred to in the ecological literature as a "climax", the second process often leads to a more or less total destruction of resources.

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2. Succession due to habitat change

The "climax" concept is undoubtedly too simple. Although the overall appearance of a climax community may seem to be constant in time, there are likely to be cyclical changes within the community (as, for example, the replacement of spruce and fir—*Picea* and *Abies*—under each other in the European spruce-fir-beech forests; and comments in *Nature* (1975) 258, 196–197). The identification of this overall form of succession in arthropod decomposer communities, in the published literature, is usually impossible for one of three reasons. First, the majority of research has been carried out in climax or near climax ecosystems. Secondly, the research not in climax ecosystems has been for too short a period of time (frequently not more than 1 to 2 years). Thirdly, studies on non-climax ecosystems have usually not been repeated on a known sequence of successional stages. Successional evidence for arthropod decomposers comes from the Moor House National Nature Reserve, an I.B.P. site in northern England. Although the blanket bog forms a type of climax ecosystem in upland regions of the British Isles, it is subjected to a cyclical process of accretion and erosion. Block (1965, 1966) and Hale (1963, 1966a, b) have documented population changes in the Acarina (mites) and Collembola (springtails) respectively. The cycle can be represented by the stages:

(1) Mixed moor (several forms)	}	Erosion
(2) Hummock top		
(3) Bare peat		
(4) <i>Eriophorum angustifolium</i>	}	Succession
(5) <i>Eriophorum vaginatum</i>		

Hale (1966b) gives qualitative data for the Collembola (except rare species) and hence only numbers of species can be used. For the third, fourth, fifth and second stages above there are 2, 17, 14 and 25 species respectively (34 species in total). Block (1966) gives population data (mean and s.e.) for only a few of the mite species, but overall there are mite densities of $0, 26.0 \pm 3.1, 34.0 \pm 3.7$ and 97.5 ± 7.2 for third, fourth, fifth and second stages respectively. Both sets of data indicate that numbers per unit area and numbers of species are likely to increase with successional age. Also on an I.B.P. blanket bog site, in Ireland, Blackith (1974) has attempted to identify individual preferences of the Collembola species, and from this to investigate the niche-widths of the various species.

A few general points can be made about the field work needed for describing successional changes in arthropod decomposer communities.

(a) The here-and-now approach, as opposed to the long-term approach, needs to be used. Ideally, it would be useful to have a long-term sampling programme on several sites, selected such that each site was a stage in the same successional sequence. Only after a number of years would it be possible to identify successional change from the year-to-year variability in arthropod population densities. A here-and-now experiment, where a number of sites in the same successional sequence were sampled, would give useful data if it were more tightly integrated than the example for blanket bogs given above.

(b) There are considerable field sampling problems due to the distribution of the arthropods into very dense aggregations. The negative binomial distribution often fits sample data well, but the implication is that a large sample size is required in order to estimate the mean population size with a reasonably small standard error. There are

also very strong seasonal changes in population density, and these are not necessarily the same from year to year.

(c) There are extraction difficulties, since the arthropods live in a three-dimensional environment that the researcher cannot see into. Each group might have to be extracted separately, which is time-consuming and destructive of the original habitat. Extraction techniques are now, however, reasonably efficient (see Phillipson, 1971).

(d) There are taxonomic problems due to the species diversity since 1 m² of soil may contain over 200 arthropod species. In Europe, taxonomy is probably not too much of a problem (except in training research staff to recognize species), but in tropical countries the taxonomic basis for many groups is lacking.

Perhaps, more importantly, the analysis of field data and the incorporation of data into more general concepts should be considered. A field programme, as described above, is purely descriptive, recording the changes in species abundance and composition but not recording the reasons for this change. Two questions can be asked. First, can realistic models of a successional change be built? These are likely to rely upon viewing succession as a Markovian process (Usher, 1973) and will be referred to again in section 4. Second, can the ideas of population dynamics, especially predator-prey and competition processes, be incorporated into our understanding of changes in abundance and species composition? This is a long-term aim of the study referred to in section 5.

3. Succession due to resource change

The fact that the majority of studies of decomposer arthropod communities have been carried out in climax or near climax ecosystems implies that the succession due to resource change can be observed directly: field results are not subject to the error of both kinds of successional influences acting at the same time. Succession due to change in the resource operates over a shorter period of time, usually only a few years, and has been more intensively studied. In the Odum (1969) sense this is not a succession at all since the end-point of the process is the destruction of resources and not a characteristic energy flow/nutrient cycle pattern. The total loss of litter in temperate deciduous woodland or tropical evergreen forests is an example. However, the decomposer communities may not totally decompose the dead organic matter (as in blanket bogs where organic matter accumulates until the erosion cycle starts) or may only decompose it very slowly (as in temperate coniferous forest systems).

In interpreting field observations on the succession of organisms on decomposing plant material, one should distinguish preference of feeding from obligate feeding. Thus the work on earthworms (e.g. Satchell and Lowe, 1967) shows that *Lumbricus terrestris* prefers certain types of leaf litter and cannot be considered to be part of a successional sequence (except in so far as it pulls leaves underground where other organisms can attack them).

Within a coniferous needle a succession has been described by Hayes (1963, 1965, 1966) who has related the physical and chemical changes to the species of Phthiracarid mites living within the needle. A more complete study, recording many groups of arthropods as well as other invertebrates and microbes, is of the decomposition of acorns of *Quercus rubra* in Illinois by Winston (1956). He describes five stages, the arthropods being particularly concerned in the later stages once larger animals have fragmented the acorn or microbes have started the decomposition process. Many other

examples of a decomposition succession could be given, such as the probability of termites attacking sapwood (Usher, 1975), microbial succession in Oklahoma forests (Mallik and Rice, 1966), or fungal succession on decomposing *Pteridium aquilinum* (Frankland, 1966).

Although more studies have been undertaken on the succession in decomposition processes, there are three questions which have not been answered adequately. First, are decomposer organisms food-specific? Hayes found that his Phthiracarid mites were not specific as to three coniferous litters (*Abies*, *Picea* and *Pinus*), but were more specific to the stage in decomposition. However, Führer (1961) found that one of Hayes' species, *Oribotritia loricata*, was strongly attracted to the rhizosphere of one plant species, *Artemisia campestris*; that water passed over dead or living *Artemisia* roots also attracted the mite; and that the attraction was probably due to a bacterium of the genus *Pseudomonas*. How specific or non-specific is the feeding of decomposer organisms?

Second, each researcher has divided decomposition into an arbitrary number of arbitrary stages: are there now enough data to form some theoretical basis for the classification of stages in the decomposition succession?

Third, there is an incredible diversity within the decomposer community, since the communities would appear to be as species-rich in the temperate regions as in the tropics. What factors contribute to the maintenance of these species-rich communities? Is this diversity due, at least in part, to the stable, or at least buffered, climatic conditions found in the soil, or, as Blackith (1974) has indicated in the Irish blanket bogs, are there a multitude of available ecological niches for these organisms?

4. Termite succession

This work in Ghana was originated by the establishment of a test site on which building materials and forest products could be exposed to determine their termite/fungus/weathering resistant properties. The site was about 0.8 ha of farm scrub (cultivation of tropical crops, mostly cassava, had ceased about six years previously). In order to make the whole site accessible, and to alleviate the danger/fear of snakes, much of the scrub was cut down so that a form of derived savanna was created (spaced bushes about 6–8 m in height, almost forming a closed canopy; a complete grass cover developed within ten months of scrub clearance). This form of vegetation, which is common near human habitation in the West African forest region, was maintained by frequent grass cutting. The study therefore relates to the change in the wood-feeding termite community during a secondary succession towards a derived savanna ecosystem.

The termite population was censused every four weeks by the use of baitwood blocks (sapwood of *Triplochiton scleroxylon*, obeche or wawa, was used). 826 blocks, spaced at 4 m by 2 m, covered the whole of the test site, and a further 100 blocks were inserted at least 4 m into the uncleared farm scrub. Records relate to the presence of termites at the blocks, presence being recorded either by seeing the termites or by inferring that they had been there by characteristic damage (nibbling) or runways. Two particular questions were of concern. First, what are the ecological characteristics of the termite community, and does it conform to the pattern of other successional communities? Second, since the site is to be used for several years for materials tests, can one predict the composition of the eventual termite community, and will it be satisfactory from the point of view of the termite hazard to which test specimens are exposed? Some basic data on the community are given by Usher (1975).

The diversity of species has been investigated both in relation to age of baitwood and length of time since clearance of the site. Graphs of the Simpson diversity index,

D , and the Simpson-Horn equitability index, E , are shown in Figures 1 and 2. Calculation of D and E are as given by May (1974):

$$D = 1/\sum p_i^2,$$

$$E = D/N,$$

where p_i is the proportion of the i th species in the community of N species. Equitability increased with succession of the habitat (during which time there was no appreciable change in the number of species present). Considering decay of the resource, the equitability increased only slightly during the first 24 weeks that a block of baitwood was in the ground, but thereafter the equitability greatly increased (and the number of species decreased). These results on a decomposer community tend to be in agreement with results on plant species diversity (e.g. Bazzaz (1975) who commented on the change from a geometric to a lognormal form of distribution; and comments in *Nature* (1975) 258, 285-286).

Markovian-type models can be built for attempting to predict the future outcome of a successional sequence (see, for example, Usher, 1973, pp. 88-91). In building a model for the termite data, the two factors of baitwood age and time since clearance have been

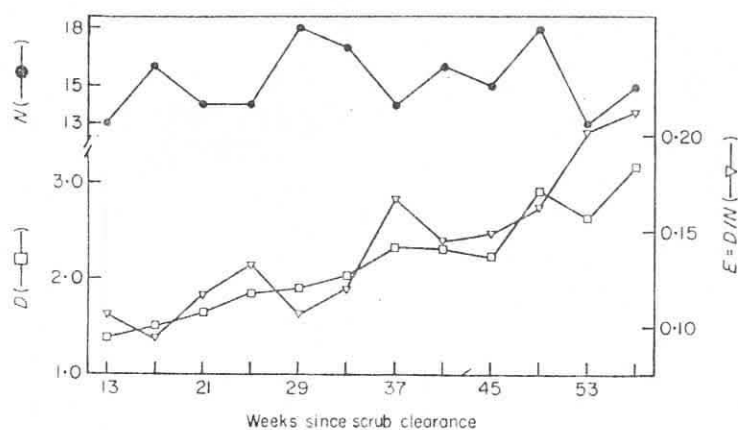


Figure 1. The relations between the length of time since scrub clearance and the Simpson diversity index (D), an equitability index (E), and the number of termite species (N).

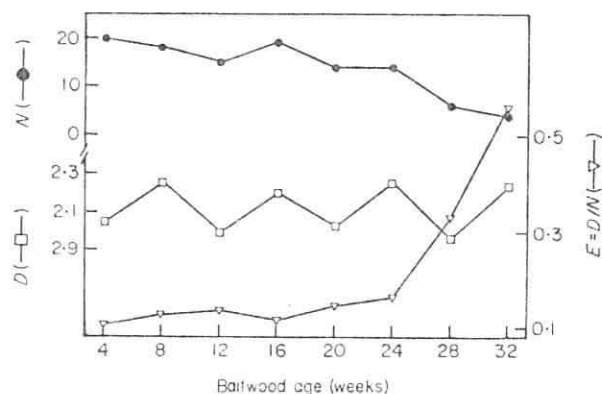


Figure 2. The relations between the age of a baitwood block (number of weeks buried in the soil) and the Simpson diversity index (D), an equitability index (E) and the number of termite species (N).

kept more or less separate. There were insufficient data for the less common species to consider each baitwood age and each length of time separately, and hence both ages and times have been grouped. A set of data is shown in Table 1.

Dividing by the row totals gives a probability transition matrix:

0.507	0.361	0.032	0.023	0.032	0.023	0.023
0.292	0.539	0.022	0.011	0.083	0.029	0.025
0.296	0.296	0.222	0.037	0.148	0	0
0.333	0.333	0	0	0.333	0	0
0.206	0.336	0.037	0.009	0.327	0.037	0.047
0.257	0.343	0	0.029	0.086	0.114	0.171
0.190	0.286	0.095	0	0.143	0.095	0.190

This matrix can be considered to have a Markovian property since the test described by Harbaugh and Bonham-Carter (1970) gives $\chi^2 = 154.31$ with 36 degrees of freedom. The matrix has a dominant eigenvalue of 1 and has a row eigenvector of

$$[1, 1.204, 0.100, 0.045, 0.272, 0.087, 0.100].$$

In order to compare predictions made for different baitwood ages and different successional times, some standardization of the eigenvector needs to be found. This can either be done by standardizing the number of baitwood blocks for which there are no termites, or by standardizing the ratio of number of termite records (the sum of terms 2, 3, ..., 7 in the vector) to the number of blocks available to the termites ($826 - k$, where k is the number with no termites). The former has been chosen, and standardized vectors are given in the Appendix.

The results of this simple model show three features of this form of modelling. First, a large amount of data are required to make the model even vaguely predict what the termite population will do. Thus, the model seems to be potentially more reliable for baitwood ages up to 8 weeks than for baitwood ages of 12 weeks and over. Second, the model does have some predictive use, since 61 weeks after scrub clearance the termite community could be represented by

$$[332, 302, 56, 87, 91, 40, 11]$$

TABLE 1. The "tally matrix" for changes observed in the termite occupation of baitwood blocks during the 2nd to 3rd and 3rd to 4th enumerations. Only baitwood ages of less than 8 weeks are included in the table

Termites on baitwood at start of 4-week period	Termites on baitwood at end of 4-week period						
	A	B	C	D	E	F	G
A. No termites	111	79	7	5	7	5	5
B. <i>Ancistrotermes</i>	162	299	12	6	46	16	14
C. <i>Macrotermes</i>	8	8	6	1	4	0	0
D. <i>Pseudacanthotermes</i>	1	1	0	0	1	0	0
E. <i>Microtermes</i>	22	36	4	1	35	4	5
F. Other termites	9	12	0	1	3	4	6
G. Unknown	4	6	2	0	3	2	4

when about 60% of baitwood was aged up to 8 weeks, 30% aged 12–16 weeks, and 10% aged 20 weeks and over. Third, such models are only of use when modelling a continuum when all the species present in the final structure are already present. Thus, *Pseudacanthotermes* was absent on the first baitwood inspection, and the model initially very much under-estimated the abundance of this species in the eigenvector. These models cannot be used to model across a discontinuity: and it is the discontinuities that classificationists have usually sought.

5. Succession in the Yorkshire Wolds

Management for wildlife conservation can be of two types: "active" or "controlled neglect". The latter is particularly suitable to climax communities where actual management interference would probably be detrimental to the ecosystem, but the former is appropriate if the aim is to conserve a successional ecosystem. The Yorkshire Wolds are, geologically, chalk laid down in the Cretaceous period, and a series of five nature reserves have been established to conserve typical Wold ecosystems. The climatic climax is ash (*Fraxinus excelsior*) woodland although at the present time a disclimax of sheep-grazed grassland predominates. Wharram Quarry reserve was established to demonstrate the successional changes, with the associated calcicole plant species. The quarry was abandoned during the period 1930–1955, resulting in a gradient of plant communities of different successional age. An investigation into the relationships between these floral communities and their associated micro-arthropod communities was begun in August 1975. Some of the initial results of this survey are presented here.

The plant frequency data, collected in August 1975 when all the plant species were visible, have been classified by Orloci's (1967) agglomerative method. On the basis of plants, there is a division into two groups, this division being spatially obvious in the successional sequence on the quarry floor. Each of these groups is further divided into two, giving at least four groups which could be equated with communities. Data for these groups are given in Table 2, where H' is the Shannon-Weaver diversity index, E is the equitability index where $E = \exp(H')/N$, and N is the number of species in each group.

If the distance from the quarry face, in Table 2, is a reasonable estimate of "successional age", then the diversity of plant species is decreasing, which is at variance with many successional studies. Imposing this plant group structure on the October 1975 arthropod data, there is a trend of increasing equitability associated with a marked trend of increasing species diversity. The collection of data on the arthropod communities will be continued since the distribution of many species is seasonal, and the abundance/scarcity of each species is not synchronous. However, these preliminary

TABLE 2. Data for plant communities at Wharram Quarry, and data for the soil arthropods found within the plant groups. H' , E and N are explained in the text

Group	Mean distance from quarry face (m)	Plants			Soil arthropods		
		H'	E	N	H'	E	N
A	19.9	2.51	0.47	26	2.87	0.34	52
B	31.3	2.32	0.38	27	3.11	0.44	51
C	73.6	2.16	0.44	20	3.18	0.44	54
D	80.4	2.24	0.52	18	3.22	0.47	53

results indicate that the decomposer diversity increases at a time when the structural change in the plant community is causing plant diversity to decrease.

What are the implications of these results for the active management of the nature reserve? By way of an answer, two further questions can be posed. First, if we manage the ecosystem for its plants, will the decomposer communities look after themselves? The data presented here indicate that in preserving the communities of high plant diversity a paucity of micro-arthropod species is likely to result. Second, do we require a diversity of decomposer organisms? If the answer is positive, then management must ensure that succession proceeds as far as the relatively species-poor grassland plant communities. If the answer is negative, then management can aim to maintain the richer, more aesthetically pleasing, plant communities. Clearly any such management question can be approached from two points of view: the policy decision as to what is or is not desirable and the scientific advice as to what will be the effects of a particular management strategy. This study on the relationships of soil arthropod and plant succession is aimed at understanding the ecological interactions, not the policy as to whether high diversity in the soil ecosystem is desirable.

6. Conclusions

In sections 2 and 3 it was shown that there are relatively few field studies which describe the two forms of decomposer succession in the field. Such studies as there are have tended to concentrate on only one group of decomposers, whereas the Wharram Quarry data indicate that the community as a whole should be investigated. A field project, looking at all groups of decomposers, could describe the successional systems, but a large amount of laboratory work would be required to identify the reasons for the change of species composition. Indeed, the amount of work involved in investigating single strands of successional systems (as shown in sections 4 and 5) is large if a sufficient replication of samples is made so as to avoid the problems of highly aggregated distribution and seasonal cycles.

Two particular aspects of successional theory have been omitted thus far from this discussion. First, in considering plant succession there is a tendency (e.g. Whittaker, 1967) to show a diagram with axes representing successional time and species abundance. There are a series of normal curves, or truncated normal curves, denoting how species composition changes. The data do not yet exist to attempt to construct such diagrams for any decomposer community. Second, the theory of "*r*-selection" and "*K*-selection" (MacArthur and Wilson, 1967) should also be applicable to decomposer organisms, both animal and microbial. When descriptive studies have progressed further, and more is known of the ordinary biology of decomposer organisms, it might be possible to investigate these more interesting aspects of the population ecology and population genetics of decomposer communities.

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Appendix: Eigenvectors derived from transition probability matrices

The derivation of these eigenvectors is discussed in section 4. The “successional time” is the number of weeks after the farm scrub had been partially cleared, and the “baitwood” age is the number of weeks that the baitwood had been in the ground subject to decomposition by micro-organisms (* at the head of a vector implies that the solution is not biologically meaningful).

Baitwood age up to 8 weeks

	Successional time (weeks)					Pooled
	17–25	25–33	33–41	41–49	49–57	
		*				
No termites	353	353	353	353	353	353
<i>Ancistrotermes</i>	425	294	350	335	348	375
<i>Macrotermes</i>	35	12	24	34	55	30
<i>Pseudacanthotermes</i>	16	21	63	85	66	46
<i>Microtermes</i>	96	70	90	101	138	97
Other termites	31	25	31	25	34	30
Unknown	35	25	11	16	14	19

Baitwood age 12-16 weeks

	Successional time (weeks)					Pooled
	17-25	25-33	33-41	41-49	49-57	
No termites	401	*	*	*	401	401
<i>Ancistrotermes</i>	341	587	617	489	395	456
<i>Macrotermes</i>	19	61	30	26	73	35
<i>Pseudacanthotermes</i>	16	52	153	101	149	79
<i>Microtermes</i>	31	44	147	112	105	71
Other termites	25	70	32	13	36	33
Unknown	21	66	40	30	21	32

Baitwood age 20 weeks and over

	Successional time (weeks)				Pooled
	25-33	33-41	41-49	49-57	
No termites	*	*		*	
<i>Ancistrotermes</i>	396	396	396	396	396
<i>Macrotermes</i>	451	584	222	450	426
<i>Pseudacanthotermes</i>	27	7	—	—	21
<i>Microtermes</i>	58	126	142	62	104
Other termites	65	72	50	114	62
Unknown	41	42	35	399	38
	62	22	24	9	36